

## Revision and new data on the Coniacian ammonite genus *Hemitissotia* in the Iberian Peninsula (Spain and Portugal)

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**Abstract** The types of the species of the Coniacian ammonite genus *Hemitissotia* Peron, 1897, identified in the Iberian Peninsula (Spain and Portugal), which are currently held in the Wiedmann (Universität Tübingen, Germany) and Choffat (Instituto Geológico e Mineiro, Portugal) collections, have been revised and refigured. New specimens of the taxa *Hemitissotia ceadouroensis* Choffat, 1898, *Hemitissotia celtiberica* Wiedmann, 1975b, *Hemitissotia turzoi* Karrenberg, 1935, *Hemitissotia dullai* (Karrenberg 1935) and *Hemitissotia lenticeratiformis* Wiedmann in Wiedmann and Kauffman, 1978 have also been presented. As results, *H. celtiberica* has been considered as a junior synonym of *H. ceadouroensis*, and the lectotype of this species and the neotypes of *H. turzoi* and *H. dullai* have been designated and figured. Additionally, the geographical and stratigraphical distributions of all of these species have been determined with precision, and several phylogenetic relationships between them have been identified,

revealing morphologies that become progressively smaller and more depressed and ornamented (hydrodynamically less efficient), interpreted as an adaptative response to sea-level changes.

**Keywords** Ammonoidea · Taxonomy · Biostratigraphy · *Hemitissotia* · Coniacian · Iberian Peninsula · Spain · Portugal

**Kurzfassung** Die Typen der Arten der Ammoniten-Gattung *Hemitissotia* Peron, 1897 aus dem Coniacium der Iberischen Halbinsel (Spanien und Portugal) wurden neu bearbeitet und abgebildet. Sie befinden sich heute in den Sammlungen von Wiedmann (Universität Tübingen, Deutschland) und Choffat (Instituto Geológico e Mineiro, Portugal). Neue Exemplare von *Hemitissotia ceadouroensis* Choffat, 1898, *Hemitissotia celtiberica* Wiedmann, 1975b, *Hemitissotia turzoi* Karrenberg, 1935, *Hemitissotia dullai* (Karrenberg 1935) und *Hemitissotia lenticeratiformis* Wiedmann in Wiedmann and Kauffman, 1978, werden ebenfalls dargestellt. Dabei zeigt sich, dass *H. celtiberica* ein jüngeres Synonym von *H. ceadouroensis* ist. Der Lectotyp dieser Arten sowie die Neotypen von *H. turzoi* und *H. dullai* werden definiert und abgebildet. Die geographische und stratigraphische Verbreitung der erwähnten Arten werden detailliert dargestellt, wie auch die phylogenetischen Beziehungen. Sie weisen eine zunehmend kleinere, flachere und stärker verzierte Morphologie auf, was hydrodynamisch weniger effizient ist und scheinbare eine Anpassung an Änderungen des Meeresspiegels darstellen.

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**Schlüsselwörter** Ammonoidea · Taxonomie · Biostratigraphie · *Hemitissotia* · Coniac · Iberische Halbinsel · Spanien · Portugal

## Introduction

Marked Late Cretaceous sea-level changes have been widely recorded in the Iberian Peninsula (especially in the Cantabrian and the Iberian ranges and the Central System, Spain, and the Beira Litoral Ranges, Portugal) by successive transgressive–regressive sequences with Boreal (from the Protoatlantic), Temperate–Warm (from the Tethys) and endemic cephalopods, which allow detailed stratigraphic settings and interregional correlations (Barroso-Barcenilla et al. 2011) and are closely related to the late Cenomanian–early Turonian and late Coniacian–early Santonian eustatic maximums (Haq et al. 1988; Hardenbol et al. 1998). Studies on the cephalopod assemblages of the late Cenomanian–early Turonian episode in these regions have been undertaken recently (Callapez 1998, 2003; Callapez and Soares 2001; Barroso-Barcenilla 2006, 2007; Barroso-Barcenilla and Goy 2007, 2009, 2010; Barroso-Barcenilla et al. 2009, 2011). In contrast, the palaeoenvironments along the Iberian Peninsula of the late Coniacian–early Santonian episode are less well understood, and previous interest has mainly focused on rudist assemblages and facies of shallow carbonate platforms (Gil et al. 2009).

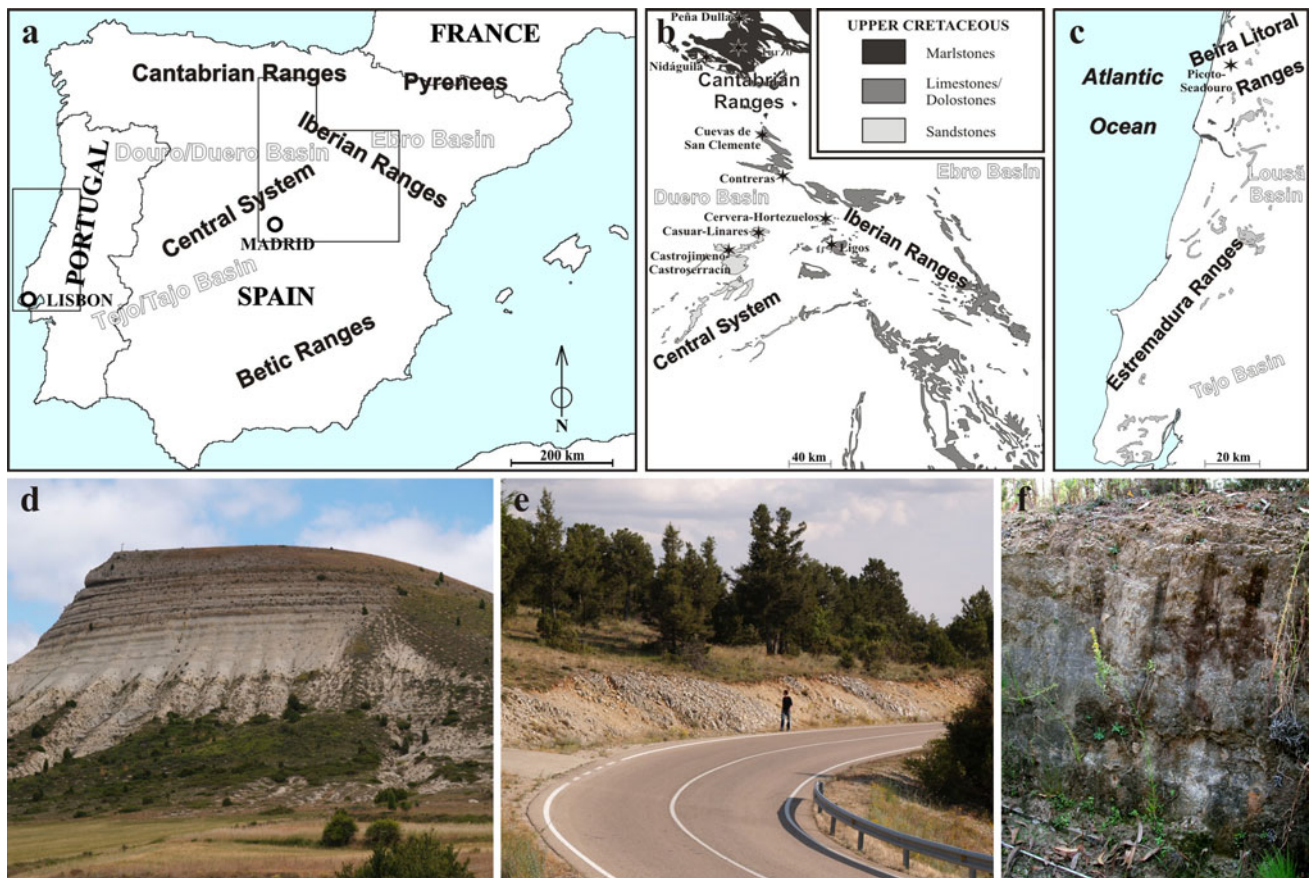
After some approaches to the cephalopod assemblages of the latter episode (Gil et al. 2008; Barroso-Barcenilla et al. 2010; García-Hidalgo et al. 2012), this work presents the first concise and joint revision of the Iberian species of the Coniacian ammonite genus *Hemitissotia* and provides new data and conclusions concerning the taxonomy, distribution and evolution of this important cephalopod group of Western Tethys. This research is based not only on the type and classic material held at the Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany, and the Museu do Instituto Geológico e Mineiro de Lisboa, Portugal, but also on new specimens recently collected in the sections of Turzo (type locality of *H. lenticeratiformis* and of the main part of the types of *H. turzoi* and *H. dullai*) and Nidáguila in the southeastern Cantabrian Ranges; of Cuevas de San Clemente, Contreras and Cervera-Hortezuelos (type locality of *H. celtiberica*) in the northwestern Iberian Ranges; of Castroserracín and Castrojimeno in the northeastern Central System, Spain; and of Picoto-Seadouro (type locality of *H. ceadouroensis*) in the western Beira Litoral Ranges, Portugal (Fig. 1a–f).

The genus *Hemitissotia* stands out as one of the most useful ammonoid groups for the Upper Cretaceous of the Iberian Peninsula, where numerous species have been described (in fact, this group will be always linked to the names of Herbert Karrenberg, Jost Wiedmann and Paul Choffat), and it has been considered a fine biostratigraphic marker for the upper Coniacian. A review of its occurrence outside the Iberian Peninsula shows that *Hemitissotia* is also one of the most relevant genera of the derived

Pseudotissotiidae, represented by characteristic forms of Tethyan keeled ammonites. The present knowledge about this group reveals a wide palaeobiogeographic distribution in a time span that ranges from the late Turonian to the early Santonian. The Iberian species of *Hemitissotia* also closely resemble some contemporary North African taxa, thus suggesting strong Tethyan faunal affinities and the prospect that future attempts at interregional correlations will be promising.

## Historical background

From the end of the nineteenth and the beginning of the twentieth centuries, numerous cephalopods were collected and described from the Upper Cretaceous of the Iberian Peninsula (among them those by Mallada 1875–1891, 1891, 1892, 1904 in Spain, and by Choffat 1886, 1898, 1900, 1901–1902 in Portugal), some of them belonging to the Coniacian genus *Hemitissotia* Peron, 1897. Among the first systematic analyses concerning this group in Spain, that of Karrenberg (1935) was the most outstanding. This author described *Hemitissotia* cf. *gallepei* Pervinquière, 1907, *Hemitissotia turzoi* Karrenberg, 1935, *Plesiotissotia dullai* Karrenberg, 1935, *Plesiotissotia dullai* var. *plana* Karrenberg, 1935 (= *H. turzoi*) and *Plesiotissotia cantabria* Karrenberg, 1935 (= *H. turzoi*) in the Cantabrian Ranges. Ciry (1940) identified *H. turzoi*, *P. dullai* and *P. cantabrica* in the Cantabrian Ranges. Bataller (1950) compiled and refigured, among others, all the species of *Hemitissotia* described to date in Spain. After collecting and studying a large number of cephalopods from the Upper Cretaceous of Spain and Portugal, Wiedmann (1960, 1964) identified *Hemitissotia ceadouroensis* Choffat, 1898, *H. cf. gallepei*, *H. turzoi*, *P. dullai* and *Hemitissotia lenticeratiformis* n. sp. in the Cantabrian and the Iberian ranges. This author also proposed the *Hemitissotia turzoi* (Co-IV) and *Hemitissotia lenticeratiformis* n. sp. (Co-V) zones as the uppermost of the Coniacian in the studied area. Wiedmann (1975a) cited *H. cf. gallepei* and *H. cf. turzoi*, and (1975b) proposed the new taxon *Hemitissotia celtiberica* in the Iberian Ranges. In the Cantabrian and the Iberian ranges, Wiedmann and Kauffman (1978) described *Hemitissotia lenticeratiformis* Wiedmann, 1978, for the first time and, like Wiedmann (1979a), identified *H. celtiberica* and *H. turzoi*. Martínez (1982) recognised *H. turzoi* in the Pyrenees. Floquet (1991) cited a significant number of representatives of *Hemitissotia* in the Cantabrian and the Iberian ranges, although he did not provide any figures. Santamaría-Zabala (1991, 1992, 1995) identified *H. turzoi* and *H. dullai* in the Cantabrian Ranges and proposed the *Hemitissotia* sp. Interval Zone (whose base is drawn by the first appearance of *H. turzoi*, and including the Co-IV and Co-V zones of



**Fig. 1** Geographic and stratigraphic provenance of the *Hemitissotia* specimens presented in this article. **a–c** Geographic general location in the Iberian Peninsula (**a**) and stratigraphic context of the main Spanish (**b**) and Portuguese (**c**) Coniacian sections studied, including other mentioned places and the lithological distribution. **d–f** Photographic views of the three most representative Coniacian outcrops

showing marlstones with chalky interbeds in Turzo (**d**), type locality of *H. lenticeratiformis* and of the main part of the types of *H. turzoi* and *H. dullai*; limestones with marly interbeds in Cervera-Hortezuelos (**e**), type locality of *H. celiberica*; and sandstones with chalky interbeds in Picoto-Seadouro (**f**), type locality of *H. ceadouroensis*

Wiedmann 1960, 1964) as the uppermost of the Coniacian in the studied area. Gallemí et al. (2007a) identified the species *H. turzoi*, *H. cf. turzoi*, *H. dullai* and *H. aff. lenticeratiformis* in the Cantabrian Ranges and recognised the *Hemitissotia* sp. Zone (also named *Hemitissotia* spp., whose index is *H. turzoi*, and corresponding to the upper part of the *Paratexanites serratomarginatus* Zone sensu Gradstein et al. 2004). Other relevant contributions to the taxonomy or biostratigraphy of the Coniacian cephalopods in Spain were made by Küchler and Ernst (1989), Gräfe and Wiedmann (1993), Martínez et al. (1996), Küchler (1998), Wiese (1997, 2000) and Gallemí et al. (2007b), but without illustrating representatives of *Hemitissotia*.

Regarding the Coniacian in Portugal, Choffat (1898) recognised for the first time that the “Senonian stage” was confined to the Beira Litoral Ranges, with a record of alluvial and marginal marine siliciclastic units with plant remains, brackish molluscs and vertebrates. The most relevant biostratigraphic data resulted from the discovery of

interbedded marine sequences with benthic palaeofauna and a few ammonites (*Hemitissotia* and *Hoplitoplacenticerias* Paulcke, 1907) near the localities of Picoto, Seadouro and Mina. These layers of “lower Senonian” (Picoto-Seadouro Sandstone with *H. ceadouroensis*) and “upper Senonian” (Mira Sandstone with *Hoplites vari* var. *marotti* Coquand, 1862) affinities proved to be a key to understand the regional stratigraphy (Choffat 1898, 1900). Specifically, the Coniacian age of the Picoto-Seadouro Sandstone (“Grés de Picoto-Siadouro” sensu Barbosa 1981) with *Hemitissotia* was first recognised by Carrington da Costa (1937). After a period without significant studies, the section was reviewed by Gutiérrez and Lauerjatz (1978), Lauerjatz and Pons (1978), Moron (1981) and Lauerjatz (1982) by means of micropalaeontology and integrated biostratigraphy. At the same time, Picoto-Seadouro was studied by Barbosa (1981) during geological field mapping. Nevertheless, the originals of *H. ceadouroensis* are still the sole available specimens of this ammonite from the type

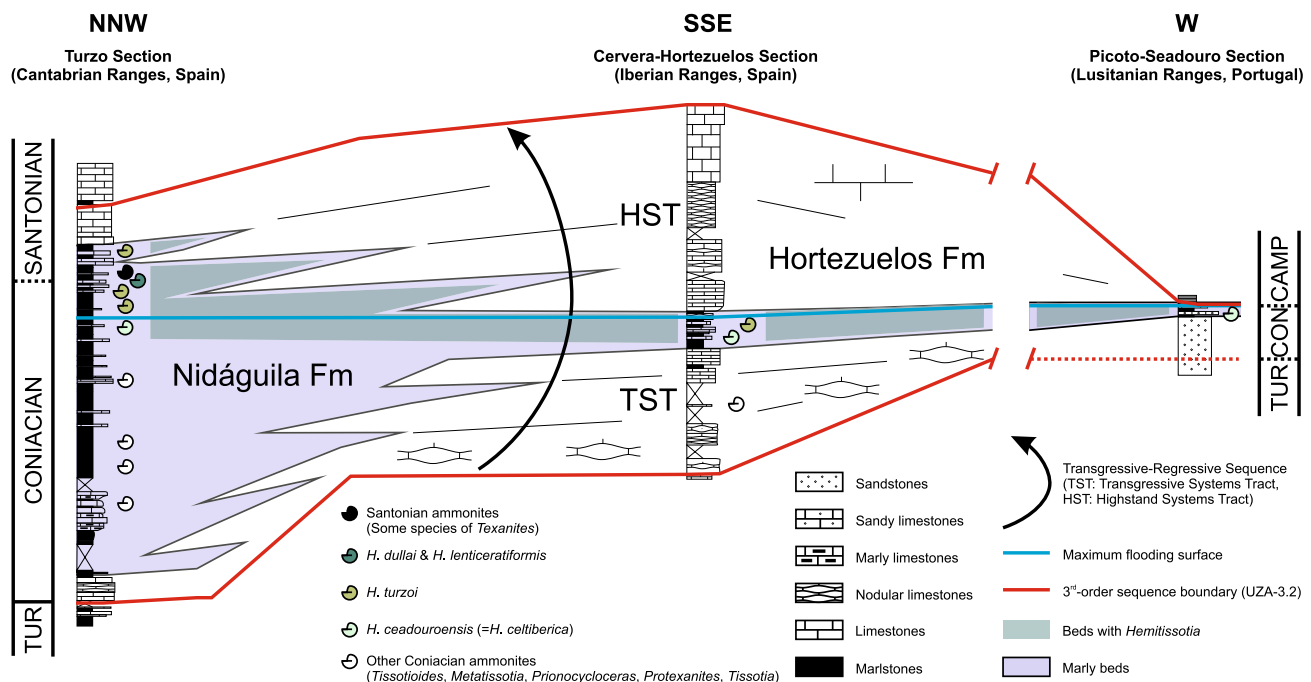
locality except for a composite mould and a fragment of a body chamber recently found and described in this article.

## Geological setting

The studied Spanish sections are part of a large northwest-southeast oriented band of Upper Cretaceous materials composed by a thick carbonate sedimentary sequence (limestones and marlstones) with some interbedded terrigenous and dolostone intervals. The Coniacian of this area is well characterised in the Cantabrian and the Iberian ranges by the stratigraphic sections of Turzo and Cervera-Hortezuelos. In Turzo (Figs. 1d, 2), the Coniacian is recorded by several beds of bioclastic limestones (10 m) with *Forresteria petrocoriensis* (Coquand 1859) and a thick interval of chalky marlstones (>100 m) with interbedded muddy limestones with numerous ammonoids, inoceramids, other molluscs and echinoids. The upper part of this thick interval yields *H. celtiberica*, *H. turzoi*, *H. dullai* and *H. lenticeratiformis* and shows a gradual upwards increase in the proportion of carbonates, culminating in several beds of limestones (10 m) with ammonites attributed to the lower Santonian (some species of *Texanites* Spath, 1932). These materials have been assigned to the Margas y Calizas Margosas de Nidáguila

Formation (Floquet et al. 1982), whose stratotype was defined by Floquet (1991) some kilometres to the south. This unit was deposited in outer platform environments and provides a complete depositional transgressive-regressive sequence with a thick Transgressive Systems Tract (TST), a maximum flooding surface (mfs) located in the upper part of the thick chalky marlstones interval and a Highstand Systems Tract (HST) characterised by the increasing carbonation of the upper part of the succession. In Cervera-Hortezuelos (Figs. 1e, 2), the Coniacian is represented by a thick interval of bioclastic and nodular limestones (40 m) with few fragments of ammonoids, echinoderms and bivalves [among them *Pycnodonte vesicularis* (Lamarck, 1806)]. It continues with an interval of limestones and marlstones (10 m) with *H. celtiberica* and *H. turzoi*, followed by a thick interval of nodular or massive limestones (60 m) with *P. vesicularis* and chalky sandstones (10 m) with scattered fragments of rudists. This is the type section of the Nidáguila Formation, and it was deposited in inner platform environments. It also constitutes a complete depositional transgressive-regressive sequence whose mfs is located in the interval of 10 m of limestones and marlstones with *Hemitissotia*.

The studied Portuguese exposures are part of a band of Upper Cretaceous materials of carbonate platform, marginal marine mixed and alluvial siliciclastic facies that



**Fig. 2** Dip cross section of the upper Turonian-lower Santonian third-order depositional sequence UZA-3.2 (sensu Haq et al. 1988) in the Iberian Peninsula, showing the depositional architecture and the main cephalopod assemblages (with lateral and ventral or dorsal views of some specimens of the most representative species) relative to the reference surfaces (maximum floodings and sequence

boundaries) and the system tracts (Transgressive Systems Tract and Highstand Systems Tract). Approximate locations of the represented composite sections (Turzo and Cervera-Hortezuelos, Spain, and Picoto-Seadouro, Portugal) and horizontal scale can be observed in Fig. 1a–c

outcrops from the Beira Litoral to the Estremadura ranges. Their Coniacian cephalopods have been mainly collected from the upper part of a thick siliciclastic unit (litostratigraphically known as “Grés de Picoto-Seadouro”), starting with littoral micaceous sandstones that gradually change upwards to coarse-grained alluvial sandstones and conglomerates, and is punctuated by a single interbedded succession of marginal marine levels with marine invertebrate fossils. This short Coniacian transgressive episode is well characterised in the Picoto-Seadouro Section (Beira Litoral Ranges, Figs. 1f, 2), which yields an interesting palaeofauna with *Hemitissotia* and other upper Coniacian molluscs (Choffat 1898, 1900). Specifically, the figured section (the original collecting place of the most of the syntypes of Choffat) is located near the site of Mina, a small local cave with an exsurgent spring. The main fossiliferous beds are coarse-grained greyish chalky sandstones (1.5 m) with diverse shell concentrations of shallow water bivalves and gastropods, including mytilids, gryphaeids and glauconiids, as well as *Hemitissotia* and cyclolitic corals. This basal sequence is overlain by laminated greyish marls (0.5 m) with small carbonised plant remains and thin whitish mudstone layers, sometimes with small cerithoid gastropods. Facies and the taphonomic imprint of mollusc concentrations suggest faunal mixing in a very shallow environment of platform coastal margin as part of a maximal extent of a flooding surface.

The correlation of these three representative successions and their interpretation in the regional context of the Iberian Peninsula shows a clear relationship between the occurrence of *Hemitissotia* in Spain and Portugal and the mfs (Fig. 2). This fact shows that the presence of this genus was related to the transgressive maximum of the Coniacian, one important relative sea-level rise of the Upper Cretaceous (Hancock 1991, 1993; Wiese and Wilmsen 1999). Additional information and references about the geological evolution of the Spanish and Portuguese Upper Cretaceous are given in Barroso-Barcenilla et al. (2011, p. 12).

### The genus *Hemitissotia* in the Iberian Peninsula

In this section, a detailed systematic account of the new records of the species assigned to the genus *Hemitissotia* Peron, 1897, is given. The terminology used for the descriptions is based on the glossary of morphological terms proposed by Barroso-Barcenilla (2008). Measurements have been made with an adjustable caliper and are given in tenths of a millimetre and in percentages of the diameter of the shell. For comments or location of refigured types (Fig. 3) and new specimens (Figs. 4, 5), the following abbreviations are used here: GPIT, Geologisches und Paläontologisches Institut der Universität Tübingen,

Germany; MIGM, Museu do Instituto Geológico e Mineiro de Lisboa, Portugal; UAH, Universidad de Alcalá de Henares, Spain; UC, Universidade de Coimbra, Portugal; UCM, Universidad Complutense de Madrid, Spain. All the specimens presented here are currently held in the Departamento de Paleontología of the UCM, the Departamento de Geología of the UAH and the Departamento de Ciências da Terra of the UC.

Superfamily Acanthoceratoidea de Grossouvre, 1894  
Family Pseudotissotiidae Hyatt, 1903

**Diagnosis** Involute shells with feeble ornamentation. During ontogeny, the ventrolateral and siphonal tubercles tend to merge, giving rise to marked keels.

**Discussion** As described in detail by Barroso-Barcenilla and Goy (2007), the taxonomical status, assignment and composition of the family has changed notably. Currently, it is generally accepted that it includes the subfamilies Pseudotissotinae Hyatt, 1903, and Hourcqiinae Renz, 1982 (Wright in Kaesler 1996).

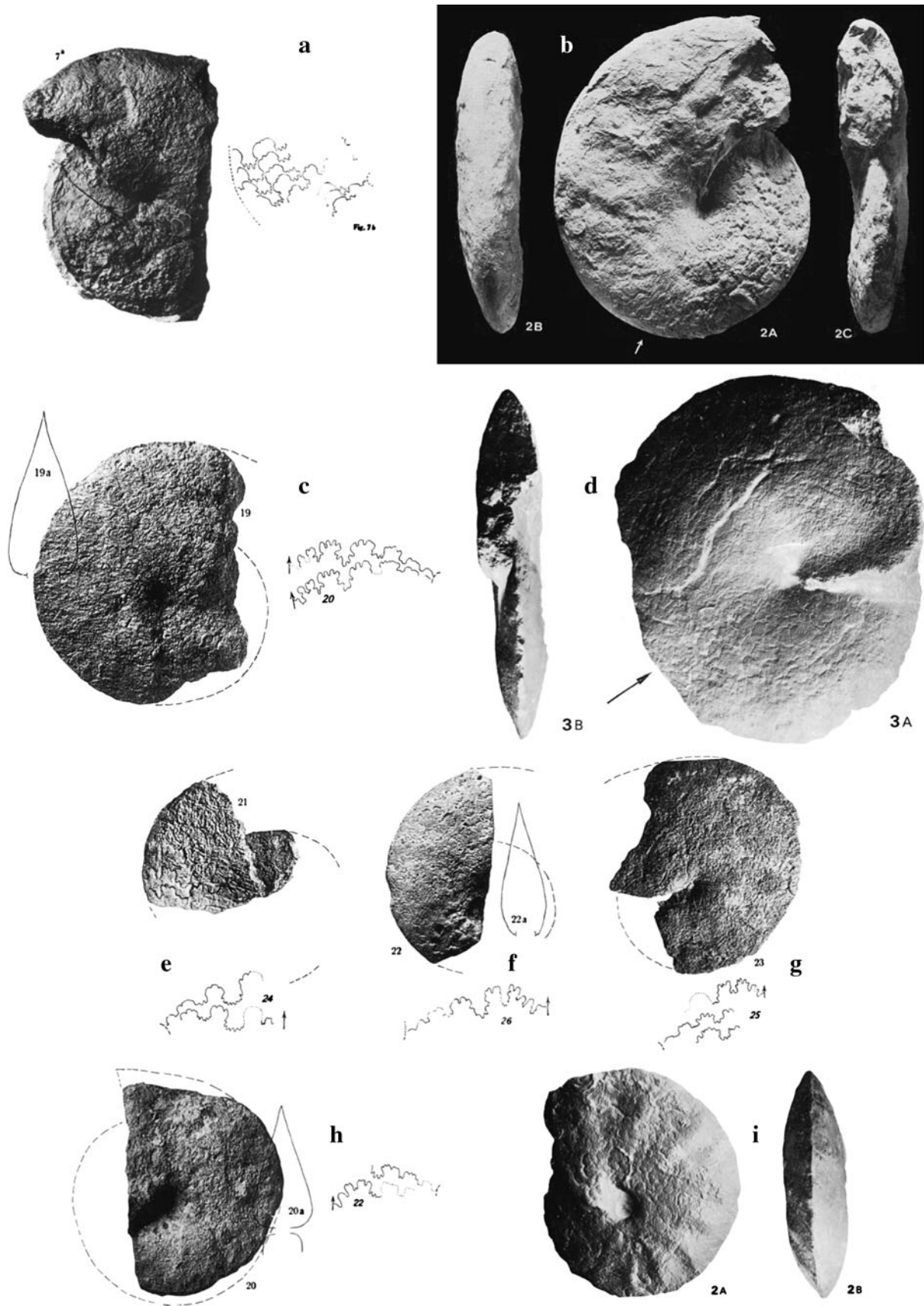
**Occurrence** From the upper Cenomanian to the lower Santonian.

Subfamily Pseudotissotiinae Hyatt, 1903 [*Nom. transl.* Wright, 1952, p. 221, *ex* Pseudotissotiidae Hyatt, 1903, p. 34. Hemitissotiinae Parnes, 1964, p. 13.]

**Diagnosis** Involute genera that usually show oxyconic morphologies with compressed whorls, tectiform or tabulate venters, flat or convex flanks and reduced ornamentations. They have wide and distant umbilical tubercles, although the last whorls are usually smooth. Some of the oldest forms of this group can preserve a globose appearance and may have ventrolateral and siphonal tubercles turning into keels in the typical subsequent taxa. Variable suture lines with a certain tendency to simplification.

**Discussion** As described in detail by Barroso-Barcenilla and Goy (2007), the taxonomical status, assignment and composition of the subfamily has changed notably. Currently, it is generally accepted that it includes the genera *Thomasites* Pervinquier, 1907, *Pseudotissotia* Peron, 1897, *Wrightoceras* Reymont, 1954, *Eotissotia* Barber, 1957, *Donenriquoceras* Wiedmann, 1960, *Choffaticeras* Hyatt, 1903, and *Hemitissotia* Peron, 1897 (Wright in Kaesler 1996).

**Occurrence** It ranges from upper Cenomanian to lower Santonian levels of numerous regions mainly belonging to the Tethyan Realm. On the Iberian Peninsula, the subfamily has been obtained in Spain from the base of the upper Cenomanian *Spathites* (*Jeanrogericeras*) *subconciatus* Zone and in Portugal from the L level of the lower Turonian *Thomasites rollandi* Zone to the lower Santonian.



◀ **Fig. 3** Types of *Hemitissotia* from the Iberian Peninsula. **a** Specimen MIGML847 of Choffat (1898, pl. 20, figs. 7a–b), designated here as lectotype of *H. ceadouroensis*. **b** Specimen GPIT1473/3 of Wiedmann (1975b, pl. 3, fig. 2a–c), holotype of *H. celtiberica* (= *H. ceadouroensis*). **c** Specimen of Karrenberg (1935, pl. 32, fig. 19–19a; pl. 33, fig. 20), designated by Santamaría-Zabala (1991, 1995) as lectotype of *H. turzoi*. **d** Specimen GPIT1456/123 of Wiedmann in Wiedmann and Kauffman (1978, pl. 22, figs. 3a–b), designated by the latter authors as hypotype of *H. turzoi*. **e** Specimen of Karrenberg (1935, pl. 32, fig. 21; pl. 33, fig. 24), syntype of *Plesiotissotia dullai* var. *plana* (= *H. turzoi*). **f, g** Specimens of Karrenberg (1935, pl. 32, figs. 22–22a, 23; pl. 33, figs. 25–26), syntypes of *Plesiotissotia cantabria* (= *H. turzoi*). **h** Specimen of Karrenberg (1935, pl. 32, fig. 20–20a; pl. 33, fig. 22), designated by Santamaría-Zabala (1991, 1995) as lectotype of *H. dullai*. **i** Specimen GPIT 1456/122 of Wiedmann in Wiedmann and Kauffman (1978, pl. 22, figs. 2a–b), holotype of *H. lenticeratiformis*. Approximately  $\times 3/5$

Genus *Hemitissotia* Peron, 1897 (*Heterammonites* Coquand, 1880, p. 39, *nom. dub.*, type species by original designation *H. ammoniticerias*; *Plesiotissotia* Peron, 1897, p. 79, type species by original designation *P. michaleti*; *Allotissotia* Parnes, 1964, p. 14, type species by original designation *Hemitissotia galleppei* Pervinquier, 1907, p. 359.)

*Type-species Hemitissotia cazini* Peron, 1897, p. 73, by original designation.

**Diagnosis** From compressed to slightly depressed ammonites with subtriangular to sublanceolate sections and sharp ventral area that can enlarge and round gradually on the mature body chamber. The first whorls may show fine ornamentation consisting of feeble umbilical tubercles and sparse and rounded ribs that tend to disappear during ontogeny. Relatively simplified suture line with five or four saddles, including a ventrolateral and a first lateral with several short indentations and the remaining three or two nearly entire.

**Discussion** Peron (1897) differentiated the new genera *Hemitissotia* and *Plesiotissotia* on the main basis that the former lacks ornamentation and exhibits five pseudoceratitic or slightly indented saddles per side, and the latter shows radial ribbing and has only four indented saddles per side. Nevertheless, as suggested by Wiedmann and Kauffman (1978) and Wiedmann (1979a) and confirmed by Santamaría-Zabala (1991, 1995), certain species of these two groups exhibit diagnostic characters of both genera, and thus *Hemitissotia* and *Plesiotissotia* can be considered synonyms. *Allotissotia* was defined by Parnes (1964) on the basis of the complete absence of ornamentation and slight differences in the suture line of this group regarding *Hemitissotia*, which does not seem enough for establishing a taxonomical group with generic rank. *Heterammonites* was considered as a *nomen dubium* by Pervinquier (1907),

Wright in Moore (1957) and Wright in Kaesler (1996), and was regarded as a synonym of *Hemitissotia*. Nevertheless, Chancellor et al. (1994) indicated that if the type species of this group, *Heterammonites ammoniticerias* Coquand, 1880, p. 39, were included within the broad morphological variability of *H. cazini*, *Heterammonites* may have priority over *Hemitissotia*. As indicated by Parnes (1964), Chancellor et al. (1994) and Wright in Moore (1996), *Hemitissotia* shows little if any significant morphologic difference from the lower Turonian subgenus *Choffaticeras* (*Leoniceras*) Douvillé, 1912. The main difference between these two groups is probably the semi-entire saddles of the former compared with the more denticular saddles of the latter.

The type species of this group, *H. cazini* Peron, 1897, initially collected from the Coniacian of Algeria, whose lectotype was designated by Chancellor et al. (1994), reaches relatively large adult size and exhibits a compressed subogival section with a relatively rounded venter and small umbilici. *H. michaleti* Peron, 1897, first identified in the Coniacian of Algeria, has a compressed subogival section with umbilici of medium width and 8–10 strong bullate umbilical tubercles per whorl that give rise to the same number of wide plications. *H. galleppei* Pervinquier, 1907, initially collected from the Coniacian of Tunisia, whose lectotype was designated by Chancellor et al. (1994), has a compressed subogival section with scaphitoid coiling, a relatively tectiform venter and wide umbilici, and exhibits sutures with an evenly divided lateral lobe without prominent adventitious lobe. *H. morreni* (Coquand, 1862), first identified in the upper Turonian of Tunisia, and *H. batnensis* Peron, 1897, regarded as synonyms by Pervinquier (1907) and Chancellor et al. (1994), reach relatively small adult size and have a notably inflated subtriangular section with conspicuous carina and a narrow stratigraphic distribution. This species was suggested as a wide variant of *Coilopoceras* Hyatt, 1903, by Robaszynski et al. (1990). *H. randoi* Gerth, 1961, initially collected from the lower Santonian of Austria, exhibit conspicuous ribbing and pseudoceratitic umbilical saddles. *H. alpina* Wiedmann, 1979b, first identified in the middle Coniacian (upper Turonian-lower Coniacian according Summesberger 1985) of Austria, shows a relatively wide and sublanceolate section, with an acute venter and maximum thickness slightly below the middle part of the flanks, and strongly incised suture lines with numerous elements. This species was suggested as a synonym of *Coilopoceras requienianum* (Orbigny 1841) by Summesberger and Kennedy (1996). *H. arumaensis* El-Asa'ad, 1991, initially collected from the Coniacian of Saudi Arabia and morphologically close to *H. galleppei*, reaches relatively large adult size and has compressed subogival to suboval sections with





◀ **Fig. 4** *Hemitissotia ceadouroensis* Choffat, 1898 (= *Hemitissotia celtiberica* Wiedmann, 1975b). **a, b** Specimen PC-S-1288, from upper Coniacian levels of Mina, near Picoto-Seadouro (type locality of *H. ceadouroensis*), Portugal; lateral (**a**) and ventral (**b**) views. **c–e** Specimen PC-S-1289 from the same stratigraphic interval of Mina; apertural (**c**), lateral (**d**) and ventral (**e**) views. **f–h** Specimen CT-S-954, from upper Coniacian levels located immediately below the *Hemitissotia turzoi* Zone sensu Wiedmann (1960, 1964) of Contreras, Spain; ventral (**f**), lateral (**g**) and apertural (**h**) views. **i–k** Specimen ST-R-958, from the same stratigraphic interval of Cervera-Hortezuelos (type locality of *H. celtiberica*), Spain; apertural (**i**), lateral (**j**) and ventral (**k**) views. **l–n** Specimen VM-R-966, from the same stratigraphic interval of Casuar-Linares, Spain; ventral (**l**), lateral (**m**) and apertural (**n**) views. Scale bar is 5 cm ( $\times 2/3$ )

scaphitoid coiling as well as a relatively rounded venter and narrow umbilici. It exhibits a suture line with six saddles per flank, the first two of which are notched or weakly incised, and the remaining four low, broad and entire.

**Occurrence** *Hemitissotia* has been cited from the upper Turonian to the lower Santonian of southern and central Europe, northern Africa, Madagascar, Israel and Saudi Arabia. All the records of this Tethyan genus seem to be related to three third-order transgressive pulses. Specifically, the stratigraphically lower forms, *H. morreni* (? = *H. batnesis*) and *H. alpina*, although considered by some authors as possible representatives of the genus *Coilopoceras*, seem to be related to the upper Turonian sea-level rise of the UZA-3.1 of Haq et al. (1988). *H. cazini*, *H. micheleti*, *H. gallepei*, *H. arumaensis* and the Iberian representatives of this genus are probably related to the upper Coniacian sea-level rise of the UZA-3.2. This interval coincides with one of the strongest transgressions of the Upper Cretaceous (Gräfe and Wiedmann 1998), and it corresponds to the maximum diversification and abundance of this genus. Finally, *H. randoi* seems to be related to the lower Santonian sea-level rise of the UZA-3.3.

*Hemitissotia ceadouroensis* Choffat, 1898, Figs. 3a, b, 4a–n

1898 *Hemitissotia ceadouroensis* Choffat: 74, pl. 20, figs. 7–10.

1935 *Hemitissotia* cf. *gallepei* [sic] Pervinquière. Karrenberg: 149, pl. 32, fig. 18; pl. 33, figs. 18–19.

1937 *Hemitissotia ceadouroensis* Choffat. Carrington da Costa: 10.

1960 *Hemitissotia* cf. *gallepei* Pervinquière. Wiedmann: 711.

1960 *Hemitissotia ceadouroensis* Choffat. Wiedmann: 723.

1964 *Hemitissotia* cf. *gallepei* Pervinquière. Wiedmann: 110.

1964 *Hemitissotia ceadouroensis* Choffat. Wiedmann: 116.

1975a *Hemitissotia* cf. *gallepei* Pervinquière. Wiedmann: 257.

1975b *Hemitissotia celtiberica* Wiedmann: 145, pl. 3, fig. 2a–c.

1978 *Hemitissotia ceadouroensis* Choffat. Gutiérrez and Lauverjat: 107.

1978 *Hemitissotia celtiberica* Wiedmann, Wiedmann and Kauffman: pl. 8, fig. 3.

1979 *Hemitissotia ceadouroensis* Choffat. Berthou and Lauverjat: 136.

1979a *Hemitissotia celtiberica* Wiedmann. Wiedmann: pl. 8, fig. 3.

1981 *Hemitissotia ceadouensis* [sic] Choffat. Barbosa: 32.

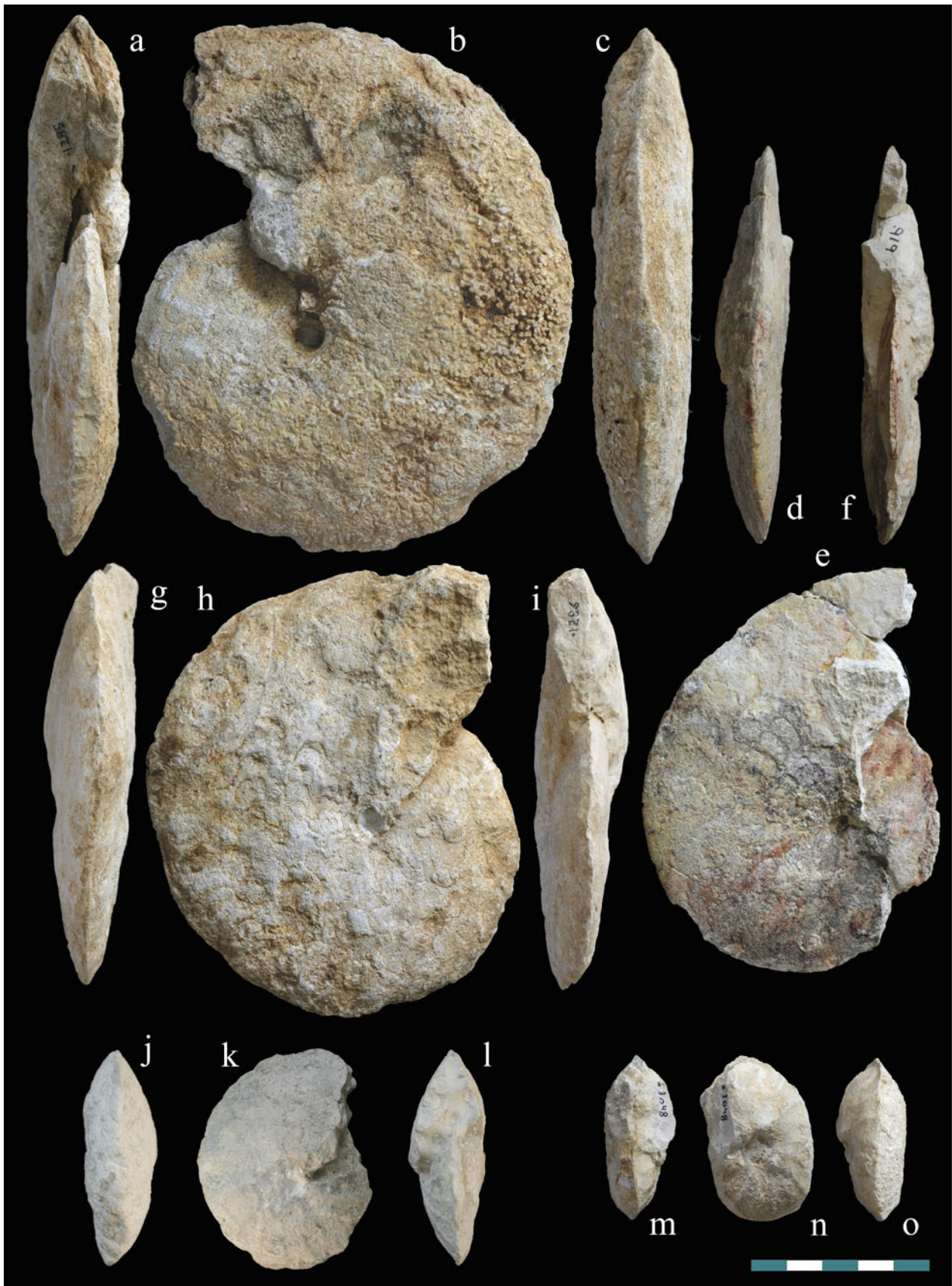
1981 *Hemitissotia ceadouroensis* Choffat. Moron: 139.

1982 *Hemitissotia ceadouroensis* Choffat. Lauverjat: 501.

1984 *Hemitissotia ceadouroensis* Choffat. Berthou: 51.

1991 *Hemitissotia ceadouroensis* Choffat. El-Asa'ad: 148.

**Types** The originals of *H. ceadouroensis* correspond to 18 specimens but, as already indicated by Choffat (1898), only 7 of them are complete and preserved enough to show the umbilicus and other diagnostic features. All of them were collected in the lower part of the Picoto-Seadouro Section and are currently held in the Choffat Collection of the MIGML. Among the two original types illustrated by this author by means of photographs, only the specimen 847, figured by Choffat (p. 74, pl. 20, figs. 7a–b) and refigured herein (Fig. 3a), preserves both umbilici and is here designated as a lectotype of *H. ceadouroensis*. Nonetheless, it must be pointed out that the original 18 syntypes of this species show certain morphological variations in both the umbilical diameter and the body chamber section. Choffat (1898, p. 74) observed this umbilical variation, mentioning seven very involute specimens with a minute umbilicus in comparison to the ammonite of plate 20, fig. 11, which is quite evolute. The 18 original specimens also suggest that typical *H. ceadouroensis* has a keeled phragmocone and a rounded body chamber with a slightly ogival whorl section (Choffat 1898, pl. 20, fig. 9). Nevertheless, there is evidence of involute specimens where the body chamber is fairly compressed and slightly keeled (Choffat 1898, pl. 20, fig. 8), resembling specimens of the younger species *H. turzoi* from Spain. Because we are dealing with a condensed section and the exposure is poor, most syntypes of Picoto-Seadouro were collected at the bed surface. Thus, it seems possible that *H. turzoi* could sporadically occur in the upper part of the section, which corresponds to a marly sequence that overlies the fossiliferous sandstone beds.



◀ **Fig. 5 a–i** *Hemitissotia turzoi* Karrenberg, 1935. **a–c** Specimen R-1285 (neotype), from the uppermost Coniacian *Hemitissotia turzoi* Zone sensu Wiedmann (1960, 1964) of Barrio Panizares, Spain; apertural (**a**), lateral (**b**) and ventral (**c**) views. **d–f** Specimen CJ-S-919, from the same stratigraphic interval of Castrojimeno, Spain; ventral (**d**), lateral (**e**) and apertural (**f**) views. **g–i** Specimen R-1286, from the same stratigraphic interval of Barrio Panizares; ventral (**g**), lateral (**h**) and apertural (**i**) views. **j–l** *Hemitissotia dullai* (Karrenberg, 1935); specimen NI-R-1214 (neotype) from the uppermost Coniacian *Hemitissotia lenticeratiformis* Zone sensu Wiedmann (1960, 1964) of Nidáguila, Spain; apertural (**j**), lateral (**k**) and ventral (**l**) views. **m–o** *Hemitissotia lenticeratiformis* Wiedmann, 1978; specimen TU-R-1048, from the uppermost Coniacian homonymous Zone sensu Wiedmann (1960, 1964) of Turzo; apertural (**m**), lateral (**n**) and ventral (**o**) views. Scale bar is 5 cm ( $\times 2/3$ )

The holotype of *H. celtiberica* is specimen 1473/3 of the Wiedmann Collection of the GPIT, obtained from the upper Coniacian at kilometre 65 of the road between Espinosa de Cervera and Hortezielos, Spain, first figured by Wiedmann (1975b, pl. 3, fig. 2a–c), and refigured herein (Fig. 3b). Unfortunately, it was impossible to locate this specimen during the recent visit of the first author of the present article to the GPIT.

**Material** 35 specimens; PC-001(1288), PC-002(1289), CJ-S-920, CJ-S-923, CJ-S-925, CJ-R-930, CJ-R-931, CJ-R-932, CJ-R-933, CJ-R-934, CJ-R-935, CJ-R-936, CJ-R-942, CJ-R-943, CJ-R-945, CJ-R-946, CJ-R-948, C1-S-953, C1-S-954, C1-R-955, C1-R-956, ST-R-958, ST-R-959, ST-R-960, ST-R-961, VM-R-965, VM-R-966, VM-R-971, LI-R-977, LI-R-978, C1-R-982, ST-R-1016, C1-R-1067, NI-R-1158 and ST-R-1287.

Dimensions	D	H (%)	E (%)	O (%)
Range	1310–630	710–345 (58–47)	345–165 (32–20)	150–55 (14–8)
Mean	965	500 (54)	255 (27)	100 (10)

**Description** This species is a rather involute and compressed, of moderately large size with a slightly eccentrically coiled adult body chamber and a very narrow umbilicus. Inner whorls have convergent and smooth, flattened sides and a sharp and almost lanceolate ventral region, which enlarges considerably on the last whorl and shows a typical round section. The suture line has five large and round saddles, the first two of which show one or two short indentations; the rest are entire.

**Discussion** Choffat (1898) recognised the morphological proximity between *H. ceadouroensis* and *Hemitissotia cazini*

Peron, 1897, but pointed out certain morphological differences between both species. Pervinquierè (1907) indicated that *H. ceadouroensis* could be a probable synonym of *Hemitissotia morreni* (Coquand, 1862), but maintained the separation of these two species. Parnes (1964) indicated that *H. ceadouroensis* is eccentrically coiled and resembles some specimens of *H. gallepei* with a small, nearly closed umbilicus. El-Asa’ad (1991) compared *H. ceadouroensis* with his new *Hemitissotia arumaensis*. Chancellor et al. (1994) stated that *H. ceadouroensis* exhibits a rounded mature venter and a more “tissotiid” suture than *H. morreni*.

Compared to the most similar species, in *H. cazini* the umbilici are wider and the suture lines are more indented. The same holds true for the remaining congeneric ammonites described by Peron (1897), as already indicated by Choffat (1898). *H. morreni* reaches smaller adult size and has a notably inflated subtriangular section with conspicuous carina and a stratigraphically lower distribution. *H. gallepei* has scaphitoid coiling, a tectiform venter and wider umbilici. *H. arumaensis* El-Asa’ad, 1991, exhibits a more depressed section and a more conspicuous carina. *H. ceadouroensis* shows a more compressed whorl section and a smaller umbilical width than *Hemitissotia turzoi* Karrenberg, 1935. In spite of these differences, both species are very similar. Although the practically continuous morphological transition between *H. ceadouroensis* and *H. turzoi* sometimes makes it difficult to distinguish both species, the latter seems to have a slightly higher and more extended vertical distribution that recommends maintaining their specific separation. *Hemitissotia turzoi* Karrenberg, 1935, has a completely smooth surface, a slightly more compressed and involute section, whose maximum width is close to the inner third of the flanks, an acute adult venter, and about two more lateral lobes and saddles per flank than *H. ceadouroensis*. In spite of these differences, *H. turzoi* and *H. ceadouroensis* are very similar, and the practically continuous morphological transition between them sometimes makes it difficult to distinguish both species (that could be considered as mere synonyms). Nonetheless, *H. turzoi* seems to have a slightly higher and more extended vertical distribution than *H. ceadouroensis*, which recommends maintaining their specific separation.

Regarding the synonymy between *H. ceadouroensis* and *H. celtiberica*, the latter form was proposed by Wiedmann (1975b) for discoidal and involute morphologies with a subogival to suboval compressed section that reaches its maximum width close to the middle part of the flanks. During juvenile stages they show an acute venter and occasionally some slight ornamentation that becomes rounded and disappears throughout ontogeny, respectively.

Sutures are pseudoceratitic, with about three indented lateral lobes and three rounded saddles per flank. *H. ceadoouroensis* thus seems to be somewhat more compressed and involute, reaching slightly larger adult size than *H. celiberica*, but these differences do not seem to justify the specific separation. Therefore, *H. celiberica* has been regarded here as a junior synonym of *H. ceadoouroensis*, and both forms can be regarded as mere geographic varieties. Wiedmann (1975b), like Wiedmann and Kauffman (1978) and Wiedmann (Wiedmann 1979a), considered the specimens classified as *H. cf. gallepei* or *H. gallepei* Pervinquière, 1907, by Karrenberg (1935) and Wiedmann (1960, 1964, 1975a) as representatives of *H. celiberica*. These specimens have thus been included here in the synonymy of *H. ceadoouroensis*.

**Occurrence** Specimens previously classified as *H. ceadoouroensis* have been reported from the upper Coniacian of Picoto-Seadouro in the Beira Litoral Ranges, Portugal, and as *H. cf. gallepei* or *H. gallepei*, or *H. celiberica* in the same stratigraphic interval of Spain. In the present work, this species has been identified immediately below and in the *Hemitissotia turzoi* Zone sensu Wiedmann (1960, 1964) (~middle? and upper, but not uppermost, part of the *Paratexanites serratomarginatus* Zone sensu Gradstein et al. 2004), in the site of Mina, near Picoto-Seadouro, Nidáguila, Contreras, Cervera-Hortezuelos, Ligos, Casuar-Linares and Castrojimeno-Castro serracín sections, showing that it is very abundant in the Iberian Ranges and the Central System of Spain.

*Hemitissotia turzoi* Karrenberg, 1935, Figs. 3c–g, 5a–i

1935 *Hemitissotia turzoi* Karrenberg: 150, pl. 32, fig. 19–19a; pl. 33, figs. 20–21.

1935 *Plesiotissotia dullai* var. *plana* Karrenberg: 151, pl. 32, fig. 21; pl. 33, fig. 24.

1935 *Plesiotissotia cantabria* Karrenberg: 152, pl. 32, figs. 22–22a, 23; pl. 33, figs. 25–26.

? 1940 *Plesiotissotia cantabrica* [sic] Karrenberg. Ciry: 213.

? 1940 *Hemitissotia turzoi* Karrenberg. Ciry: 213.

1945 *Plesiotissotia cantabrica* [sic] Karrenberg. Bataler: 133, fig. 743.

1945 *Plesiotissotia dullai* var. *plana* Karrenberg. Bataler: 135, fig. 745.

1945 *Hemitissotia turzoi* Karrenberg. Bataller: 135, fig. 746.

1949 *Hemitissotia turzoi* Karrenberg. Hourcq: 104, figs. 1–1a.

1949 *Plesiotissotia cantabria* Karrenberg. Hourcq: 104, figs. 3–3a.

cf. 1960 *Hemitissotia cf. turzoi* Karrenberg. Wiedmann: 711, 716, 722.

1960 *Hemitissotia turzoi* Karrenberg. Wiedmann: 717, 719, 721, 722.

cf. 1964 *Hemitissotia cf. turzoi* Karrenberg. Wiedmann: 110, 113, 116.

1964 *Hemitissotia turzoi* Karrenberg. Wiedmann: 113–116.

cf. 1975a *Hemitissotia cf. turzoi* Karrenberg. Wiedmann: 257.

1977 *Hemitissotia turzoi* Karrenberg. El-Asa'ad: 304, pl. 24, figs. 2a–b.

1978 *Hemitissotia turzoi* Karrenberg. Wiedmann and Kauffman: pl. 12, figs. 3a–b.

1979a *Hemitissotia turzoi* Karrenberg. Wiedmann: pl. 12, figs. 3a–b.

1982 *Hemitissotia turzoi* Karrenberg. Martínez: 131, pl. 22, fig. 5.

1991 *Hemitissotia turzoi* Karrenberg. Santamaría-Zabala: 170, pl. 11, fig. 7.

cf. 1991 *Hemitissotia cf. turzoi* Karrenberg. Santamaría-Zabala: 174.

1991 *Hemitissotia turzoi* Karrenberg. El-Asa'ad: 143, pl. 1, figs. 1–4.

1995 *Hemitissotia turzoi* Karrenberg. Santamaría-Zabala: 58, pl. 5, fig. 1; fig. 1k.

2007a *Hemitissotia turzoi* Karrenberg. Gallemí et al.: 98.

**Types** The lectotype designated by Santamaría-Zabala (1991, 1995) is the original of Karrenberg (1935, pl. 32, fig. 19–19a; pl. 33, fig. 20) from the upper Coniacian of Castreñas, Spain, refigured herein (Fig. 3c). The remaining original specimen of Karrenberg (1935, pl. 33, fig. 21) is from the upper Coniacian of Turzo, Spain. Unfortunately, as indicated by Wiedmann (1960, 1964), all the original specimens of Karrenberg were destroyed during World War II. The hypotype designated by Wiedmann and Kauffman (1978) and Wiedmann (1979a) is specimen 1456/123 of the Wiedmann Collection of the GPIT, obtained from the uppermost Coniacian (Co-IV Zone of Wiedmann 1960, 1964) of Terradillos de Sedano, Spain, first figured by Wiedmann in Wiedmann and Kauffman (1978, pl. 22, figs. 3a–b) and refigured herein (Fig. 3d). The specimen R-1285 (Fig. 5a–c) from the upper Coniacian of Barrio Panizares is here designated as the neotype. It is currently held in the Departamento de Paleontología of the UCM.

**Material** 28 specimens; CJ-S-919, CJ-S-924, CJ-S-928, TU-R-988, TU-R-989, TU-R-999, TU-R-1007, TU-R-1010, TU-S-1022, TU-S-1023, TU-R-1047, TU-R-1051, TU-R-1059, TU-R-1061, TU-R-1063, TU-R-1068, TU-R-1069, TU-R-1070, TU-R-1071, TU-R-1072, TU-R-1073, SC-S-1118, NI-R-1157, NI-S-1220, NI-R-1221, NI-R-1237, R-1285 and R-1286.

Dimensions	D	H (%)	E (%)	O (%)
Range	1,600–495	870–270 (64–54)	300–115 (27–15)	100–30 (7–5)
Mean	900	510 (58)	185 (21)	55 (6)

**Description** Very compressed and involute species with subogival or sublanceolate whorl section, whose maximum width is close to the inner third of the flanks. Its suture lines are pseudoceratitic and variable, having five or four wide saddles per flank and deep lobes.

**Discussion** *P. dullai* var. *plana* and *P. cantabria*, only established by small differences in the suture line and whose types are refigured herein (Fig. 3e–g), can be considered as mere synonyms of *H. turzoi*, as indicated by Santamaría-Zabala (1991, 1995). *H. turzoi* is similar to the close species *Hemitissotia ceadouroensis* Choffat, 1898 (= *Hemitissotia celtiberica* Wiedmann, 1975b), as detailed above. Among the remaining species of the genus, *H. cazini* Peron, 1897, exhibits a relatively similar morphology, but this species has a more rounded and less compressed whorl section compared to *H. turzoi*.

Morphologically, *H. turzoi* exhibits numerous features close to those characterizing *Eulophoceras* Hyatt, 1903, and this species, along with *Hemitissotia dullai* (Karrenberg, 1935), was included in this genus by Hourcq (1949). In fact, *H. turzoi* is difficult to differentiate from the lower Santonian *Eulophoceras losaense* Santamaría-Zabala, 1995, but the latter species exhibits juvenile ornamentation composed of tenuous ribs and more irregular suture lines.

**Occurrence** This species has been identified in the uppermost Coniacian *Hemitissotia turzoi* and *Hemitissotia lenticeratifformis* zones sensu Wiedmann (1960, 1964) (~ upper part of the *Paratexanites serratomarginatus* Zone sensu Gradstein et al. 2004) and in the lowermost Santonian of the Cantabrian Ranges and the Pyrenees. In fact, *H. turzoi* has been considered an index species of the uppermost Coniacian by several authors, such as Gischler et al. (1994) and Gräfe et al. (2002). Outside Spain, specimens attributed to *H. turzoi* have been reported from Saudi Arabia by El-Asa'ad (1977, 1991). El-Asa'ad (1991) also indicated the presence of one ammonite (F-11667) from the “lower Senonian” of Morocco attributed to this species in the Sedgwick Museum of Cambridge University, UK. Hourcq (1949) described several forms very close to *H. turzoi* from Madagascar. In the research presented here, this species was identified in the same stratigraphic interval of the Turzo, Nidáguila, Cuevas de San Clemente and Castrojimeno-Castroterracedín sections, showing that it is very abundant in the uppermost Coniacian of the

Cantabrian Ranges of Spain. However, there are less numerous records from the lowermost Santonian and from other regions of the Tethyan Realm.

*Hemitissotia dullai* (Karrenberg, 1935) Figs. 3h, 5j–l

1935 *Plesiotissotia dullai* Karrenberg: 151, pl. 32, fig. 20–20a; pl. 33, figs. 22–23.

non 1935 *Plesiotissotia dullai* var. *plana* Karrenberg: 151, pl. 32, fig. 21; pl. 33, fig. 24. [= *H. turzoi*]

? 1940 *Plesiotissotia dullai* Karrenberg. Ciry: 213, pl. 7, figs. 1–1a, 2.

1945 *Plesiotissotia dullai* Karrenberg. Bataller: 134, fig. 744.

non 1945 *Plesiotissotia dullai* var. *plana* Karrenberg. Bataller: 135, fig. 745.

1949 *Plesiotissotia dullai* Karrenberg. Hourcq: 104, figs. 2–2a.

1960 *Plesiotissotia dullai* Karrenberg. Wiedmann: 711, 717, 719, 721.

1964 *Plesiotissotia dullai* Karrenberg. Wiedmann: 110, 113–115.

1991 *Hemitissotia dullai* (Karrenberg). Santamaría-Zabala: 174, pl. 10, fig. 3.

1995 *Hemitissotia dullai* (Karrenberg). Santamaría-Zabala: 60, pl. 4, fig. 2; fig. 1m.

2007a *Hemitissotia dullai* (Karrenberg). Gallemí et al.: 98, fig. 8b.

**Types** The lectotype designated by Santamaría-Zabala (1991, 1995) is the original of Karrenberg (1935, pl. 32, fig. 20–20a; pl. 33, fig. 22), from the upper Coniacian of Peña Dulla, Spain, refigured herein (Fig. 3h). The remaining original specimens of Karrenberg (1935, pl. 33, fig. 23, and non-figured) are from the upper Coniacian of Turzo and Soncillo, Spain. Unfortunately, as indicated by Wiedmann (1960, 1964), the original specimens of Karrenberg were destroyed during World War II. The specimen NI-R-1214 (Fig. 5j–l) from the uppermost Coniacian of Nidáguila is here designated as the neotype. It is currently held in the Departamento de Paleontología of the UCM.

**Material** 2 specimens; NI-R-1214 and NI-R-1229.

Dimensions	D	H (%)	E (%)	O (%)
NI-R-1214	600	355 (59)	~ 230 (~ 38)	45 (8)
NI-R-1229	760	450 (59)	~ 350 (~ 46)	85 (11)

**Description** Small, involute, compressed and slightly inflated specimens with sublanceolate section and greatest

whorl breadth close to the umbilical margins. Small and deep umbilici with flat, high and sloping walls and sharp umbilical shoulders. They lack adult ornamentation and have relatively simple suture lines with four saddles per flank with few incisions; the first one is divided by a deep lobe.

**Discussion** Ciry (1940) emended the definition of this species and included *Plesiotissotia cantabria* Karrenberg, 1935, and *Hemitissotia turzoi* Karrenberg, 1935, in its morphologic variability. On the contrary, Floquet (1991) considered *H. dullai* as a synonym of *H. turzoi*. Although there is an almost continuous morphological transition between *H. dullai* and *H. turzoi* (including the existence of intermediate forms, as that figured by Ciry 1940, pl. 7, figs. 1-1a), the former seems to have a wider whorl section with sharper umbilical shoulders, a smaller adult size and a shorter vertical distribution, which recommend maintaining their specific separation. Among the remaining species of the genus, only *H. morreni* (Coquand, 1862) exhibits a relatively close morphology, but shows a notably more inflated subtriangular section with conspicuous carina than *H. dullai*.

**Occurrence** Specimens of *H. dullai* have been collected in stratigraphic levels corresponding to the uppermost Coniacian *Hemitissotia lenticeratiformis* Zone sensu Wiedmann (1960, 1964) (~uppermost part of the *Paratexanites serratomarginatus* Zone sensu Gradstein et al. 2004) of the Cantabrian Ranges, Spain. In the present work, *H. dullai* has been identified in the same interval of the Nidáguila Section in the Cantabrian Ranges.

*Hemitissotia lenticeratiformis* Wiedmann in Wiedmann and Kauffman, 1978, Figs. 3i, 5m–o

1960 *Hemitissotia lenticeratiformis* n. sp. [sic] Wiedmann: 718, 722.

1964 *Hemitissotia lenticeratiformis* n. sp. [sic] Wiedmann: 114, 116.

1978 *Hemitissotia lenticeratiformis* Wiedmann in Wiedmann and Kauffman: pl. 12, figs. 2a–b.

1979a *Hemitissotia lenticeratiformis* Wiedmann in Wiedmann and Kauffman, Wiedmann: pl. 12, figs. 2a–b. aff. 1982 *Hemitissotia lenticeratiformis* Wiedmann in Wiedmann and Kauffman. Martínez: 132, pl. 23, figs. 1a–b.

aff. 2007a *Hemitissotia* aff. *lenticeratiformis* Wiedmann in Wiedmann and Kauffman. Gallemí et al.: 98.

**Types** The holotype is specimen 1456/122 of the Wiedmann Collection of the GPIT, from the uppermost Coniacian (Co-V Zone of Wiedmann 1960, 1964) near Turzo, Spain, first figured by Wiedmann in Wiedmann and Kauffman (1978, pl. 22, figs. 2a–b) and refigured herein (Fig. 3i).

**Material** 2 specimens; TU-R-1048 and TU-R-1057.

Dimensions	D	H (%)	E (%)	O (%)
TU-R-1048	460	230 (50)	~200 (~43)	70 (15)
TU-R-1057	–	–	~170	~50

**Description** Small, involute, compressed and slightly inflated specimens with sublanceolate section and greatest whorl breadth close to the umbilical margins. Small and deep umbilici with flat and sloping walls and sharp umbilical shoulders. They have 12 blunt and straight plications per whorl, especially marked near the ventral area, and a relatively simple suture line with four saddles per flank with few incisions.

**Discussion** Regarding the generic assignment of this species, Wiedmann and Kauffman (1978) and Wiedmann (1979a) stated that it exhibits intermediate characteristics between *Hemitissotia* and *Lenticeras* Gerhardt, 1897. As indicated by Wiedmann and Kauffman (1978) and Wiedmann Wiedmann (1979a), *H. lenticeratiformis* is close to *Hemitissotia michaleti* Peron, 1897, but the latter shows sharper primary and secondary ribs. *Hemitissotia morreni* Coquand, 1862, and its synonym *Hemitissotia batnensis* Peron, 1897, exhibit more inflated whorls. *Hemitissotia randoi* Gerth, 1961, shows different ribbing and pseudo-ceratic umbilical saddles. As already indicated by its author, the specimen of Martínez (1982, pl. 23, figs. 1a–b) and maybe the non-figured of Gallemí et al. (2007a, p. 98) exhibit slightly different coiling and more tenuous and flexuous plications, and could be a representative of a different taxon.

**Occurrence** Specimens of *H. lenticeratiformis* have been identified in stratigraphic levels corresponding to the uppermost Coniacian homonymous Zone sensu Wiedmann (1960, 1964) of the Cantabrian Ranges, Spain, being considered the index species of this interval by several authors, such as Gischler et al. (1994) and Gräfe et al. (2002). In the research presented here, *H. lenticeratiformis* was collected in the same interval of the Turzo Section in the Cantabrian Ranges.

## Conclusions

The types of the species of the Coniacian ammonite genus *Hemitissotia* Peron, 1897, identified in the Iberian Peninsula (Spain and Portugal), which are currently held in the Wiedmann (Universität Tübingen, Germany) and Choffat (Instituto Geológico e Mineiro, Portugal) collections, have been revised and refigured. Unfortunately, it was

impossible to include the original specimens of the Karrenberg Collection in this study because they were destroyed during World War II. However, numerous new specimens of the taxa *Hemitissotia ceadourensis* Choffat, 1900, *Hemitissotia celtiberica* Wiedmann, 1975b, *Hemitissotia turzoi* Karrenberg, 1935, *Hemitissotia dullai* (Karrenberg, 1935) and *Hemitissotia lenticeratiformis* Wiedmann in Wiedmann and Kauffman, 1978, have been collected in several Spanish (e.g., Turzo, type locality of *H. lenticeratiformis* and of the main part of the types of *H. turzoi* and *H. dullai*, and Cervera-Hortezuelos, type locality of *H. celtiberica*) and Portuguese (e.g., Picoto-Seadouro, type locality of *H. ceadourensis*) sections and are presented here. *H. celtiberica* has been considered as a junior synonym of *H. ceadourensis*, and the lectotype of this species, and the neotypes of *H. turzoi* and *H. dullai* have been designated and figured.

The stratigraphical and geographical distribution of *Hemitissotia* in this region has been determined with precision; it occurs in the upper Coniacian (~upper part of the *Paratexanites serratomarginatus* Zone) with sporadic records in the lowermost Santonian. Specifically, *H. ceadourensis* (= *H. celtiberica*) was identified immediately below and in the *Hemitissotia turzoi* Zone sensu Wiedmann (1960, 1964) (~middle? and upper, but not uppermost, part of the *Paratexanites serratomarginatus* Zone), being very abundant in the Iberian Ranges and the Central System of Spain and less common in the Beira Litoral Ranges of Portugal. *H. turzoi* has been collected in the *Hemitissotia turzoi* and *Hemitissotia lenticeratiformis* zones sensu Wiedmann (1960, 1964) (~upper part of the *Paratexanites serratomarginatus* Zone) and in the lowermost Santonian, being very abundant in the Cantabrian Ranges of Spain. *H. dullai* has been identified in the *Hemitissotia lenticeratiformis* Zone sensu Wiedmann (1960, 1964) (~uppermost part of the *Paratexanites serratomarginatus* Zone) of the Cantabrian Ranges of Spain, and *H. lenticeratiformis* has been identified in the same stratigraphic and geographic intervals. The records of *H. ceadourensis* and the acme of *H. turzoi* seem to be related to the maximum flooding surface (mfs) of the third-order sequence UZA-3.2 (sensu Haq et al. 1988), whereas the records of *H. dullai* and *H. lenticeratiformis* seem to be related to the Highstand Systems Tract (HST) of the same cycle. In terms of the phylogeny of the group, one possible evolutionary lineage joining *H. turzoi* with *H. dullai* and *H. lenticeratiformis* has been identified, revealing morphologies that become progressively smaller and more depressed and ornamented (hydrodynamically less efficient ammonites: Chamberlain 1980; Westermann 1996). These morphological changes seem to be adaptative responses to the sea-level oscillations (ecophenotypic variations: Wilmsen and Mosavinia, 2011), specifically to the shallowing related to the change from the maximum flooding to the HST.

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